FORAGE & GRAZING LANDS

Variation between Alamo and Cave-in-Rock Switchgrass in Response to Photoperiod Extension

G. A. Van Esbroeck, M. A. Hussey, and M. A. Sanderson*

ABSTRACT

The length of the growing period for switchgrass (*Panicum virgatum* L.) can vary considerably across environments. For many species, phenotypic plasticity for length of the vegetative phase results from a photoperiod mediated transition from vegetative to reproductive development. The objective of this study was to determine the effects of photoperiod on tiller development on a northern (Cave-in-Rock) and southern (Alamo) switchgrass cultivar. Plants were removed from the field and grown in greenhouses during winter at natural (11.5–13 h) and extended (16 h; 12 h natural + 4 h light extension) photoperiods. Photoperiod extension was with 100 μmol m^{-2} s^{-1} of photosynthetic photon flux density. For Cave-in-Rock at a 16-h photoperiod, panicle emergence was delayed by 18 d (39% longer than at the 12-h photoperiod) and the duration of panicle exsertion was extended by 17 d (243% longer than at the 12-h photoperiod). The delay in panicle emergence for Cave-in-Rock was associated with an increase in the phyllochron, whereas the total number of leaves on a tiller was not affected. Extended photoperiod did not alter time to panicle emergence in Alamo; however, the duration of panicle exsertion was extended by 15 d (136%). A delay in development under long photoperiods in both cultivars suggested a facultative short-day response; however, photoperiod did not appear to affect the initiation of reproductive development but rather extended the period of panicle exsertion. Photoperiod has a large effect on growth and development of switchgrass cultivars affecting their forage or biomass production value. Forage production of switchgrass in short-day environments may be improved with cultivars that are less photoperiod sensitive.

I N MANY FORAGE CROPS, including switchgrass, biomass yields are maximized in cultivars with a long growing period (Newell, 1968; Hopkins et al., 1995) or long leaf area duration (Madakadze et al., 1998a). For switchgrass, however, a great deal of phenotypic plasticity exists for the length of vegetative development (Sanderson and Wolf, 1995). Photoperiod is a major factor influencing the transition of the apical meristem from a vegetative to a floral state (Vince-Prue, 1975) and has a major influence on the duration of vegetative growth in annual cereals (Russell and Stuber, 1983; Miglietta, 1989; Collinson et al., 1992). Although switchgrass is a perennial species, it is similar to determinate annual crops because it normally initiates only a single cohort of tillers in spring if not defoliated (Hyder, 1974).

Most C$_4$ grasses are short-day plants that require short days to flower (obligate short-day plants) or flower earlier under short days (facultative short-day plants). When short-day grasses are grown in long days, floral initiation is delayed and leaf production continues resulting in more leaves at maturity (Quinby, 1972). Differences in final leaf number have been used to assess photoperiodic response (Halloran, 1977; Russell and Stuber, 1983). In some species, photoperiod also affects the rate of leaf development (Kiniry et al., 1991).

Cooper (1960), citing the work of Benedict (1940) and Gardner and Loomis (1953), listed switchgrass as a short-day plant with no vernalization requirement. However, it is not clear which geographical strains were used in these studies. Response to photoperiod in native North American grasses often varies widely within species with a wide geographical distribution. For example, in selections of blue grama (*Bouteloua curtipendula* Michx. Torr.) originating from North Dakota to Texas, a range from long-day to short-day plants was observed; northern types were long-day, several Oklahoma types were intermediate in their photoperiod response, and the Texas types were short-day (Olmsted, 1944).

Some switchgrass cultivars may be sensitive to photoperiod because plants flower at the same time each year despite differences in temperature (Hopkins et al., 1995; Sanderson and Wolf, 1995). Several reports, which indicated that the total number of leaves produced on tillers varies across locations and years (Redfearn et al., 1997; Madakadze et al., 1998b) or between spring growth and summer regrowth (Van Esbroeck et al., 1997), also suggested that switchgrass is sensitive to photoperiod. A better understanding of the role of photoperiod on the duration of growth of individual tillers among switchgrass lines may aid in the development or use of cultivars that can fully utilize the growing season. The objective of this study was to determine the effects of photoperiod on leaf and floral development for a southern (Alamo) and northern (Cave-in-Rock) switchgrass cultivar.

MATERIALS AND METHODS

Greenhouse studies were performed on the switchgrass cultivars Cave-in-Rock and Alamo during the winter and early spring at College Station, TX. Cave-in-Rock originated in Illinois (40° N latitude), whereas Alamo originated in south Texas (29° N) (Alderson and Sharp, 1994). Dormant sods (10 by 10 by 10 cm) were removed from established field plots (January and February) at College Station, TX (30° N) and immediately planted into 2.7-L pots containing a commercial soil mix. Pots were kept at natural daylength in the greenhouse. New tillers emerged 2 to 3 wk after plants were brought inside. At this time 12 pots per cultivar were randomly ar-

ranged within an ambient (about 12 h) and an extended (16 h) photoperiod treatment. Photoperiod treatments were placed at the ends of two greenhouses. To create the extended photoperiod treatment, plants at one end of the greenhouse were supplied with an additional 5 h of light (sodium halide lamps that supplied 100 μmol m^{-2} s^{-1} of photosynthetic photon flux density at plant level with a red:far-red ratio of 2.37). Supplemental lighting was turned on from 1h before sunset to 4 h after sunset to give an approximate 4-h photoperiod extension. Shade cloth was used to prevent supplemental light from reaching the control plants. During photoperiod extension, light levels for the ambient photoperiod (darkness) were less than 0.1 μmol m^{-2} s^{-1} of PPFD at plant level. Plants receiving the 12-h photoperiod were kept at the opposite end of the greenhouse. Every 3 wk, the locations of the photoperiod treatments within the greenhouse were reversed to eliminate potential temperature differences among the treatments.

The experiment was performed simultaneously in two greenhouses at two starting dates (5 Jan. and 1 Feb. 1996). One of the greenhouses was equipped with a heater, whereas both had daytime cooling. Each starting date–greenhouse combination (trial) was considered a block for a total of four blocks. The experimental design was a factorial arrangement of a randomized complete block. Cultivar and photoperiod effects were considered fixed and blocks random.

Ambient photoperiods (civil sunrise to civil sunset) between transplanting and panicle emergence ranged from 11.5 to 13 h. Temperatures were recorded with hygrothermographs within each greenhouse. Mean daily temperature was determined by averaging the greenhouse air temperatures at 0300, 0900, 1500, and 2100 h. Growing degree days (GDD) were calculated as: Σ (mean daily temperature $-10°$C).

When plants had two visible leaves they were thinned to five tillers per pot and one tiller per pot was tagged. Numbers of visible leaf tips on the tagged tillers were recorded weekly. For each cultivar–photoperiod–trial combination, the mean number of leaves per tiller was regressed on GDD and second-order polynomial regression equations were obtained using the REG procedure from SAS (1991). Regression equations were solved to determine the GDD for the appearance of each leaf. The phyllochron for each leaf was determined as the additional GDD required to produce that leaf beyond the previous leaf.

All tillers in each pot were observed every 3 d for stage of panicle emergence. Percent panicle emergence was determined as the average number of flowering tillers (of the initial five per pot) in a block. Final leaf number, time of panicle emergence, time of complete panicle exsertion (node of the lowermost panicle branch visible above the collar), and final panicle length (tip to node of lowermost panicle branch) were recorded on the first tiller (of the original five) in each pot that produced a panicle. If panicles had not completely exserted within 30 d after emergence, complete panicle exsertion was arbitrarily set to 3 d beyond the last sampling date and

panicle length determined by dissection. At the completion of the study, the length and width (at the midpoint of the lamina) of the fifth leaf lamina (counting from the base) and the height to the collar of the uppermost fully extended leaf was measured on all tagged tillers. All tillers per pot were clipped and dry matter determined after drying for 3 d at 70°C. Data for the 12 pots of each photoperiod-cultivar combination within a block were averaged for analysis.

For phyllochron, percentage flowering tillers, and dry matter, data for the 12 pots of each photoperiod-cultivar combination within a block were averaged for analysis. For the remaining traits, pots were considered subsamples. Failure of some plants to produce floral tillers resulted in unequal subsample numbers for floral data (final leaf number, days to panicle emergence, days to complete panicle exsertion, and panicle length). Thus, these data were analyzed with the GLM procedure in SAS (1991), which calculated F ratios by means of an approximate mean square for the error term. An F-protected least significant difference ($P = 0.05$) was used for mean separation.

RESULTS AND DISCUSSION

Air temperatures in the greenhouses ranged between 10 and 29°C at night and between 15 and 43°C during the day with mean temperatures for the four trials of: 26.5, 22.7, 27.0, and 24.6°C. After thinning to five tillers per pot, few subsequent tillers developed and all data were recorded from the original five tillers. For Alamo, many of the plants in one of the trials had not completely exserted panicles by 1 May when natural daylengths approached 14 h. Thus, only three trials were used in the analysis of floral data for Alamo.

There were several significant interactions between cultivar and photoperiod for leaf and floral development (Tables 1, 2, and 3). There was a large cultivar $\times$ photoperiod interaction ($P < 0.01$) for time to panicle emergence. At the 16-h photoperiod, panicle emergence in Cave-in-Rock was delayed by 18 d (39%) compared with the 12-h photoperiod, whereas in Alamo this trait was not affected by photoperiod (Table 1). For both cultivars, however, the percentage of tillers that produced panicles nearly doubled at the 16-h photoperiod compared with the 12-h photoperiod. Nada (1980) also observed heading in switchgrass under a range of photoperiods (9, 12, and 15 h) but heading was delayed at 9 and 15 h. McMillan (1959) did not observe flowering of switchgrass at 10 h but abundant flowering at 14- and 15.5-h photoperiods.

Variation in the length of the vegetative phase may be mediated through the phyllochron and/or the total

Table 1. The effect of photoperiod on tiller and panicle development of Cave-in-Rock and Alamo switchgrass.

Cultivar	Photoperiod	Flowering tillers	Final leaf number	Time to panicle emergence†	Time to complete panicle exsertion†	Final panicle length
	h	%	no.	d		cm
Cave-in-Rock	12	40	7.0	46	53	12
	16	83	7.7	64	88	36
Alamo	12	46	9.8	84	95	25
	16	87	7.6	82	108	55
Cultivar $\times$ photoperiod LSD(0.05) †		29	0.7	8	7	5

† Days from the 2-leaf stage.
† Least significant difference ($P = 0.05$) for comparing photoperiods within a cultivar.

Table 2. The effect of photoperiod on the phyllochron (growing degree days, base 10°C) for sequential leaves of Cave-in-Rock and Alamo switchgrass.

Cultivar	Photoperiod	Leaf number			
		Three	Four	Five	Six
	h	— Growing degree days† —			
Cave-in-Rock	12	78	80	82	85
	16	103	113	129	158
Alamo	12	173	178	185	196
	16	146	159	177	204
Cultivar × photoperiod					
LSD (0.05)‡		28	23	22	37

† Growing degree days (GDD) were calculated as: Σ (mean daily temperature −10°C).
‡ Least significant difference (P = 0.05) for comparing photoperiods within a cultivar.

Table 3. The effect of photoperiod on lamina size of Leaf 5, stem height and weight per tiller for Cave-in-Rock and Alamo switchgrass.

Cultivar	Photoperiod	Lamina length	Lamina width	Stem height†	Weight per tiller
	h	— cm —			g
Cave-in-Rock	12	26	0.78	41	0.55
	16	34	0.97	51	1.40
Alamo	12	43	1.19	90	3.79
	16	47	1.02	84	3.53
Cultivar × photoperiod					
LSD(0.05)‡		4	0.11	13	0.50

† Height to uppermost leaf collar.
‡ Least significant difference (P = 0.05) for comparing photoperiods within a cultivar.

number of leaves produced (Frank and Bauer, 1995). For Cave-in-Rock, delayed panicle emergence at long photoperiods was not associated with a significant change in final leaf number. The phyllochron of Cave-in-Rock was longer at the 16-h photoperiod than the 12-h photoperiod (Table 2). This difference increased from 32% (25 GDD per leaf) at Leaf 3 to 86% (73 GDD per leaf) at Leaf 6. The longer phyllochron for Cave-in-Rock at the 16-h photoperiod was associated with an increase in leaf size; final lamina length increased by 30% and lamina width increased by 24% (Table 3). Leaf number was not linearly related to GDD as is generally reported in cereals (Frank and Bauer, 1995) but the phyllochron (number of GDD per leaf) increased as leaf number increased (Table 2). This trend was also observed in other studies with perennial grasses (Frank and Hofmann, 1989; Skinner and Nelson, 1995; Van Esbroeck et al., 1997). Quadratic regressions of mean leaf number on GDD resulted in coefficients of multiple determination of 0.98 or greater for all cultivars and trials. Other photoperiodic effects included a 24% increase in stem height and a 150% increase in tiller weight for Cave-in-Rock at 16- versus 12-h photoperiods (Table 3).

A delay in development under long days in Cave-in-Rock suggested that it is a facultative short-day plant. Its response, however, is not typical of many common short-day species. First, the percentage of flowering tillers did not increase under short days. This may have been due to the reduced light and generally smaller plant size under short-day conditions. Second, delays in flowering for Cave-in-Rock were not related to a substantially greater number of leaves indicating that the transition from vegetative to reproductive growth was unaffected by photoperiod. Delays in flowering, however, were related to alterations in leaf development. Our result showing a greater leaf lamina length for Cave-in-Rock under long photoperiods suggests that the longer phyllochron may be related to a greater lamina length. A longer leaf lamina is normally associated with a longer leaf sheath, which increases the distance a new leaf must extend to become visible and thus may contribute to a reduced leaf appearance rate (Skinner and Nelson, 1995). It would also delay the appearance of the panicle.

These data for Cave-in-Rock, showing delays in flowering mediated through alterations in leaf development

but not total leaf number, are in contrast with more typical short-day responses in C_4 grasses. Delayed flowering at long photoperiods for black grama [*Bouteloua eriopoda* (Torr.) Torr], corn (*Zea mays* L.), and grain sorghum [*Sorghum bicolor* (L.) Moench] was associated with delayed floral initiation and continued production of leaves, which resulted in a greater total number of leaves at maturity (Quinby, 1972; Russell and Stuber, 1983; Schwartz and Koller, 1975). Earlier panicle emergence for switchgrass regrowth compared with spring growth was also associated with fewer leaves on the mainstem (Van Esbroeck et al., 1997). However, earlier panicle emergence for northern than southern cultivars was primarily associated with a higher leaf appearance rate as all cultivars produced panicles after a relatively similar number of leaves had appeared (Van Esbroeck et al., 1997).

Time to panicle emergence in Alamo was not affected by photoperiod (Table 1). Final leaf number was reduced at the 16-h photoperiod suggesting earlier floral initiation. Earlier floral initiation may have resulted from additional radiant energy at long photoperiods, which can enhance floral initiation in C_4 grasses (Burson, 1980). The phyllochron of Alamo was not significantly affected by photoperiod; however, the phyllochron increased with increased leaf number (Table 2). For Alamo, leaf lamina length and stem height were not affected by photoperiod; however, leaf width was reduced by 14% at the 16-h photoperiod (Table 3). Some of these effects may have been indirectly related to greater radiation input or increased flowering at the extended photoperiod. Most perennial grasses begin stem extension when the apex becomes reproductive. Stem extension in switchgrass, however, is not triggered by floral initiation; rather it elevates a vegetative apical meristem (Branson, 1953). Therefore, it is presumed that inflorescence development had minimal effect on leaf and stem growth.

In this study, the influence of photoperiod did not end at panicle emergence. At the 16-h photoperiod, the duration of panicle exsertion (panicle emergence to complete exsertion) was increased by 17 d (243% longer than at the 12-h photoperiod) for Cave-in-Rock and by 15 d (136% longer than at the 12-h photoperod) for Alamo (Table 1). For both cultivars, the extended duration of panicle exsertion was associated with a two to three fold increase in panicle length (Table 1). Although

photoperiod can affect all stages of development (Vince-Prue, 1975), reports on the effects of photoperiod on postfloral initiation are few. Some photoperiod sensitive genes in sorghum increased the panicle development phase by 60% (Quinby, 1972). McMillan (1965) reported that in Texas, northern switchgrass ecotypes produced short panicles in the spring and fall and large panicles in mid-summer. In rice (*Oryza* sativa L.), some degree of photoperiod sensitivity often continues into the panicle development stage (Collinson et al., 1992).

The duration of the panicle exsertion phase for both cultivars ranged from 7 to 26 d and accounted for up to 30% of the time from the 2-leaf stage to complete panicle exsertion. An increase in this period could be advantageous in that it could maximize seed production; however, the effects of an extended panicle development phase on biomass accumulation are not known. Presumably leaf aging and senescence reduces photosynthetic output and limits biomass accumulation during this period. In the field, we have observed culm elongation until complete panicle exsertion, indicating that some biomass accumulation probably occurs during the panicle exsertion phase.

A delay in the time to complete panicle exsertion at the 16-h photoperiod for both Alamo and Cave-in-Rock (Table 1) confirmed previous reports (Cooper, 1960) that showed switchgrass to be a short-day species. Our study also showed that switchgrass is similar to many other perennial C_4 grasses of the Great Plains where photoperiod sensitivity is greatest in northern ecotypes (Olmsted, 1944). In contrast to numerous other cereals and grasses, photoperiod did not appear to influence the time of transition from vegetative to reproductive growth. Rather, photoperiodic influences were observed primarily on the duration of panicle growth and panicle size. Further study appears warranted on the effect of an extended period of panicle development on biomass accumulation.

Environmental variation in flowering time for switchgrass does not appear to be a simple response to photoperiod. In the field, it may not be possible to separate the effects of photoperiod on flowering from other environmental factors. Long photoperiods in this study were associated with both delayed flowering in Cave-in-Rock and a higher percentage of flowering tillers in both Cave-in-Rock and Alamo. Moreover, long daylengths are usually associated with increased radiant energy and higher temperatures, factors that generally speed up floral initiation in C_4 species (Burson, 1980). When exposed to similar photoperiods, greenhouse-grown plants usually flower at an earlier leaf stage than field-grown plants (Van Esbroeck et al., 1998) providing further evidence that factors other than photoperiod influence floral initiation.

The most northern cultivar, Cave-in-Rock, showed the greatest sensitivity to photoperiod with the length of the vegetative phase (2-leaf stage to panicle emergence) extended by 39% at a 16- versus a 12-h photoperiod. Variation in sensitivity to photoperiod may affect the relative potential of these species for biomass production. For example, at a 12-h photoperiod the vegetative

phase was 83% greater for Alamo than Cave-in-Rock, whereas at a 16-h photoperiod the vegetative phase was only 28% longer. This may explain the early panicle emergence and low yields for Cave-in-Rock when grown in southern locations (Sanderson and Wolf, 1995; Sanderson et al., 1996). Moreover, the reduced leaf area expansion and dry matter accumulation at short photoperiods may account for the limited late-summer and fall growth of Cave-in-Rock in Texas (Sanderson et al., 1996). This study suggests that the large effect of photoperiod on the growth and development of some switchgrass cultivars has a major effect on their relative value for forage production. Greater utilization of less photoperiod-sensitive cultivars of switchgrass may improve forage production in short-daylength environments. Although we have shown differential responses of Alamo and Cave-in-Rock to photoperiod, more detailed studies appear necessary to determine whether developmental delays at extended photoperiods are a true photoperiodic response or are the result of an indirect effect on vegetative morphology.

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